THE UNIVERSITY OF ALBERTA

CAECAL FUNCTION IN GALLIFORM BIRDS WITH SPECIAL REFERENCE TO JAPANESE QUAIL

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1972

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Caecal function in galliform birds with special reference to Japanese quail" submitted by Lois Fenna in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

The function of the caeca in galliform birds was investigated by the use of Japanese quail (*Coturnix coturnix*).

In a controlled experiment, involving 120 Japanese quail, the caeca were excised from a proportion of the birds and all were subjected to diets of differing fibre content and to contrasting temperatures. Further investigation into alimentary changes at low temperatures was made.

Contrast radiography was employed as a technique for demonstrating activity in the quail's intestine. The structure of the caecum was also examined.

It was found that quail were not adversely affected by caecectomy, but that intact birds developed enlarged caeca when subjected to low temperatures. X-ray studies revealed retrograde peristalsis in the large intestine, which was interpreted as a probable mechanism for filling of the caeca.

It was concluded that the caeca are important components of the alimentary canal in herbivorous Galliformes, but that fermentation of cellulose is not a major function. It is postulated that they are responsible for the terminal phases in digestion and absorption of basic nutrients following separation of these from undigestible fibre. This separation seems to be performed during retrograde peristalsis of the large intestine, which causes liquid intestinal contents to be directed through the narrow caecal ducts, while fibrous material is prevented from

entering by the meshwork of villi, and forms instead the fibrous intestinal faeces.

ACKNOWLEDGEMENTS

I should like to thank my supervisor, Dr. D. A. Boag, and the other members of my committee for the assistance they have given me in carrying out this project.

I am indebted to Dr. T. Overton of the Division of Biomedical Engineering and Dr. J. Miller, Chairman of the Radiology Department of the Faculty of Medicine, for making their machines and technicians available for the X-ray studies.

Dr. B. Chernick advised me on the preparation of the tables, and Dr. J. Lauber provided histological advice and equipment.

I wish to thank Dr. Boag for help in preparing the manuscript, and my husband for assistance in proofreading.

This research was supported in part by a grant from the Province of Alberta.

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INTRODUCTION

Avian caeca are paired blind pouches communicating with the main alimentary tract at the junction of small and large intestines, where they form an acute angle with the adjacent small intestine. They are vestigial in some orders and absent in others, including parrots, swifts, and swallows, but extremely well developed in owls, ducks, and gallinaceous birds (Marshall 1960). Those with the greatest development are herbaceous feeders and in addition rely for long periods of time on green vegetation rather than fruits and seeds. In fact, a direct relation has been established between the length of the caeca and the type of diet in the same species of birds (Leopold 1953, Lewin 1963, Pendergast and Boag, in press), the caeca being longer during the period (usually winter) that the birds are dependent on herbaceous or woody green vegetation.

Caecal function is still a controversial subject. Many functions have been postulated and results of experiments are still inconclusive. Physiological and nutritional experiments have been confined largely to galliform birds, mainly the domestic fowl, and have included investigations into vitamin synthesis (Jackson *et al.* 1955, Sunde *et al.* 1950), water absorption (Olson and Mann 1935), protein digestion (Payne 1967), production and absorption of fatty acids (McBee and West 1969, Barber 1968), and microbial digestion of fibre, in particular the cellulose fraction (Thornburn and Wilcox 1965, Moss and Parkinson 1972, Suomalainen and Arhimo 1945). A potentiality for digestion, or a slight decrease in digestibility

following extirpation of the organs has been demonstrated, but no actual absorption from the caecum of any particular nutritional substance has been shown.

Recent digestibility studies on fibre in spruce grouse and ptarmigan have exacerbated the controversy by indicating on the one hand a very minor degree of fibre digestibility (Pulliainen *et al.* 1968, Pendergast and Boag 1970) and on the other, a more extensive digestion of fibre, especially at times of dietary stress (Moss and Parkinson 1972). The caecum was suggested as the site for this process.

This study was initiated to investigate the role of the caeca in digestion under laboratory conditions, and since grouse are unsuitable for experiments demanding large numbers of birds, Japanese quail (*Coturnix coturnix*) were chosen as laboratory subjects.

METHODS

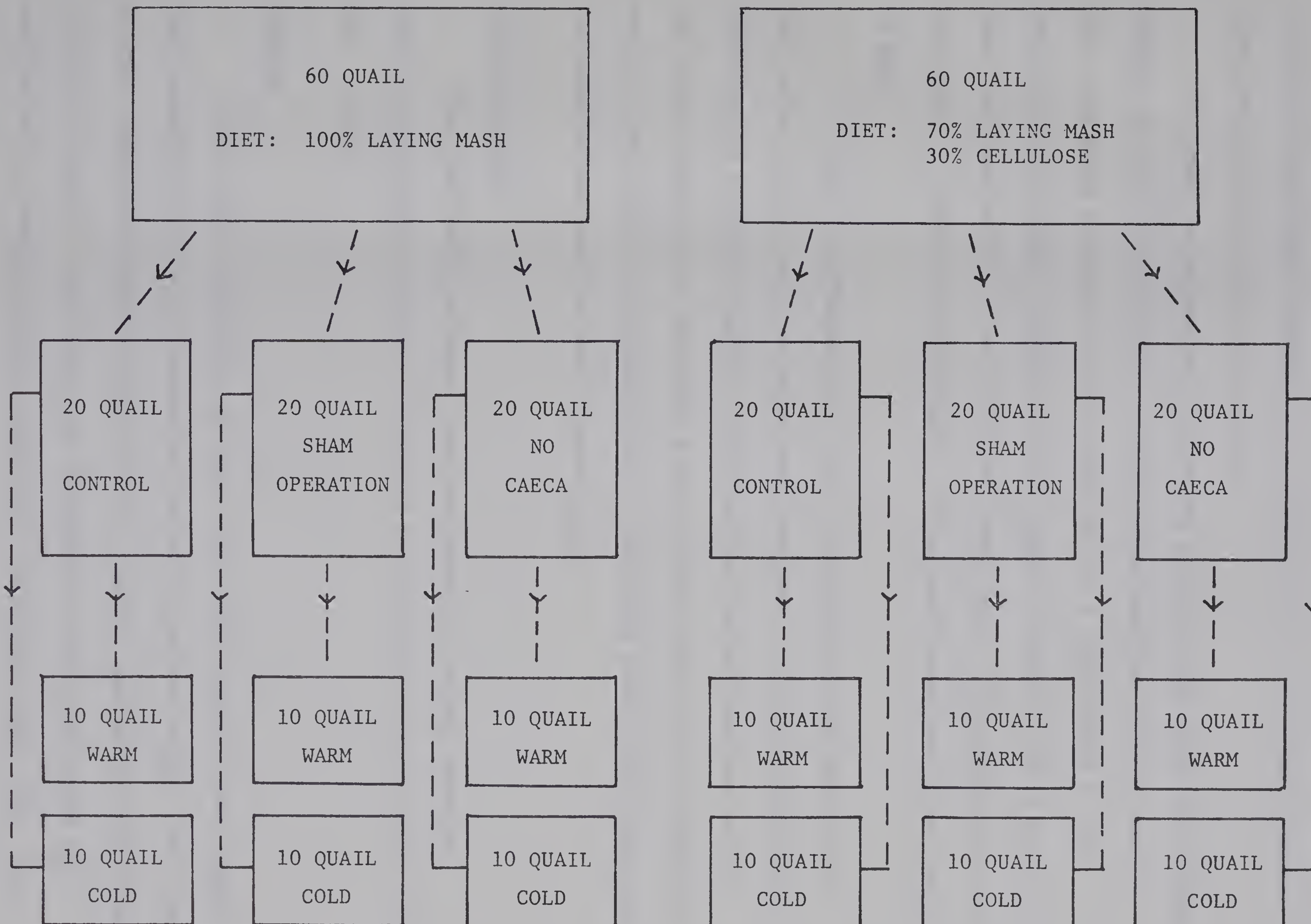
Experimental Design

There are two features which seem to characterise the birds with enlarged caeca, one being the reliance on green vegetation and the other being the ability to survive periods of presumed thermal stress when ambient temperatures fall significantly, while subsisting on such a diet. If the caeca are important in fibre digestion it was postulated that differences in fibre content of the diet would show measurable differences (for example in body weight, survival, anatomy of the intestine) between intact birds and birds that had been subjected to caecectomy, particularly if environmentally stressed by low temperature.

In the first experiment (Fig. 1), two groups of 60 male Japanese quail were introduced to diets containing, respectively, large and small quantities of cellulose fibre (see below). Six weeks later one-third of the birds in each group were deprived of caeca, by excision, one-third received a sham operation, and the remaining third were left intact to act as a control group. All birds were held an additional four weeks for recovery.

Half of each group of 20 birds were transferred to a controlled environment chamber, so that ten out of each group of operated (sham and caecectomised) and intact birds, on both high and low fibre diets, were subjected to a temperature initially of 10° C, while the remaining half were kept at approximately 23° C. After two weeks, the temperature in the

Figure 1. Design of first experiment to show effect of caecectomy on quail under different conditions of diet and temperature


60 QUAIL
DIET: 100% LAYING MASH
60 QUAIL
DIET: 70% LAYING MASH
30% CELLULOSE
20 QUAIL
CONTROL
20 QUAIL
SHAM
OPERATION
20 QUAIL
NO
CAECA
20 QUAIL
CONTROL
20 QUAIL
SHAM
OPERATION
20 QUAIL
NO
CAECA
10 QUAIL
WARM
10 QUAIL
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COLD
10 QUAIL
COLD

controlled environment chamber was lowered to 2° C, and after a further three weeks all the birds were killed.

In order to determine the rate and point in time when the observed changes in the quail occurred, a second experiment was begun. Twenty-five male quail were kept for two weeks at 23° C, then moved to the controlled environment chamber and kept there at first at 10° C for one week, and then at 2-5° C for a further seven weeks. Two birds were killed each week in order that measurements of the gastrointestinal tract could be made.

To further investigate the role of nutrition in the dynamics of the caeca, a third and final experiment was made. Forty male quail were subjected to a similar regime, differing from the previous one only to the extent that half of them were given a high protein poultry mash diet and the other half a low protein diet. Four birds were killed each week for examination, two from each dietary group.

Origin of Birds

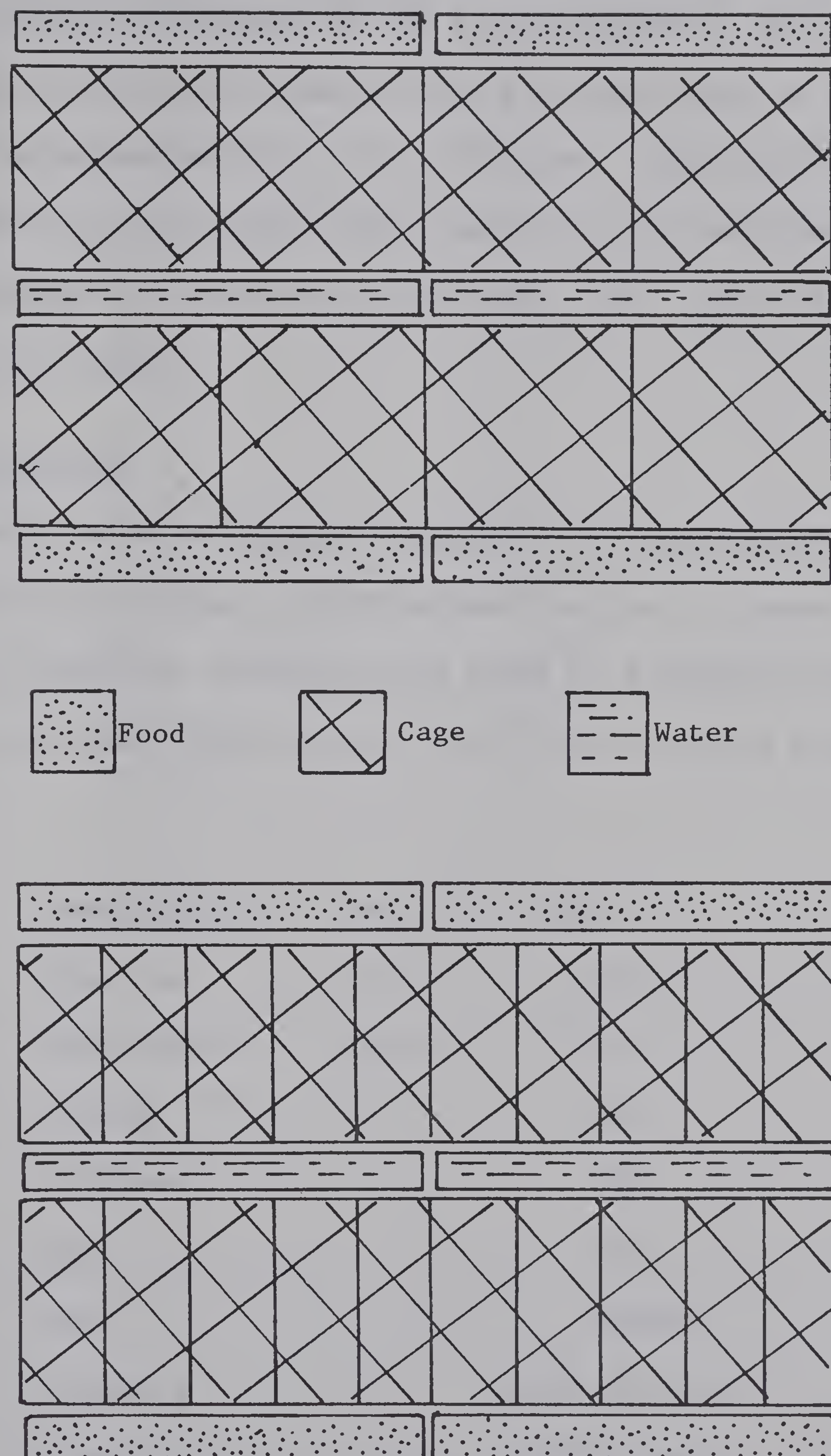
The quail were purchased from the University Animal Breeding Centre at Ellerslie, Alberta. They were all approximately six weeks old when received.

Housing

In the first experiment the birds were first housed in wire cages, each measuring 12 x 12 x 8 inches and joined in racks of eight, four side by side, separated from the other four by a central passageway containing the water troughs. Five birds were allocated to each cage, which was serviced with a feeding trough shared with the adjacent cage (Fig. 2A).

Figure 2A. Plan view of cages in which quail were housed initially in first experiment

Figure 2B. Plan view of individual cages used in place of group housing


Food
Cage
Water

Differences in aggressiveness among birds housed in groups led to considerable loss of plumage, several deaths and noticeable differential feeding. Thus after two months of the first experiment, and for the entire second and third experiments, each bird was housed in an individual cage, measuring approximately 6 x 10 x 8 inches. These were built on an average of ten to a row, being linked, as were the group cages, by a central passageway to another row behind (Fig. 2B). One food container now supplied five cages.

Feeding and Watering

Unlimited water was supplied throughout the experiments, all birds drinking from the containers placed between the rows of cages.

Feed in the first experiment was based on a prepared poultry food, laying mash, the components of which were in the following minimum proportions:

Crude protein	(min)	16%
Crude fat	(min)	2.67%
Crude fibre	(max)	6.5%
Calcium		1.45%
Phosphorus		.85%
Salt		.5%
Zinc		.0028%
Vitamin A		5,000 IU per lb
Vitamin D		1,000 IU per lb

No antibiotics or other medication are added to the mixture.

This was given in unlimited quantities to 60 of the birds; the remaining 60 received a mixture containing 70% of this laying mash and 30% of a synthetic cellulose preparation ("Alpha Floc"--Brown Co., Boston).

The feed was weighed each time the containers were refilled, so that the amount of food consumed each week could be calculated.

In the second experiment all birds were given a diet of prepared poultry food, turkey starter, which had a minimum composition of:

Protein	26%
Crude fat	3%
Fibre	6%
Salt	0.35%
Calcium	1.35%
Phosphorus	1.3%
Vitamin A	4,500 IU per lb
Vitamin D_3	1,300 IU per lb

In the third experiment half of the birds were fed on laying mash and the other half on turkey starter.

Surgery

The operations were performed under local anaesthesia, using approximately 0.5 ml of 1% "Xylocaine" injected subcutaneously in the abdominal region.

The birds, which were not fasted prior to surgery, were partially immobilised by means of a small sock over the head and wings; they were held supine on a board using cotton ties on the legs and an elastic band

across the end of the sock, beyond the head.

For the sham operations a small area of the abdominal skin was plucked, a midline incision was made, and extended anteriorly and obliquely to the right. The peritoneum was opened and the duodenum and pancreas were seen to be presenting. This loop was moved gently to one side, and a loop of intestine hooked out from the right lower quadrant. Usually this included the two caeca, lying closely attached by a very short mesentery to the side of the small intestine. The junction with the intestine was impossible to see, being situated close to the dorsal wall of the abdomen and anterior to the highest point of the incision. After inspection, the gut was returned to the cavity, the peritoneum and abdominal wall closed separately with interrupted silk sutures, and the quail put into an individual cage to recuperate.

For the caecectomies, mobilisation was accomplished by cutting through the mesenteries between caeca and small intestine, some bleeding being encountered during this process. It ceased after compression with gauze paper swabs, but it was obvious that this degree of trauma and manipulation was exerting considerable strain on the bird. When as much caecum as seemed possible had been mobilised, it was clamped with a haemostat, and the proximal end secured with a 5-0 silk suture on an atraumatic needle. The caecum was then removed and the proximal end closed off with the suture. The second one was removed in a similar way. When all bleeding had stopped, the gut was replaced and the wound closed as before. The birds were allowed to recuperate in individual cages for two days before replacing them in the original cages. Mortality resulting from surgical procedures is given in Appendix 2.

Radiography

An investigation into caecal action in quail was made by X-ray contrast photography. Three-quarters of a ml of barium sulphate suspension was introduced into the oesophagous of a bird by means of a syringe fitted with a short polythene catheter. The bird was then restrained in the supine position adopted for the surgical approach, and placed on an X-ray table beneath an image-intensifying fluoroscope. This instrument uses a small dose of radiation and permits direct vision of the part to be photographed. The process of passage of the barium through the gut was observed, and photographs taken at various stages (Plates 1-3). A videotape record was also made of parts of the procedure, and subsequently edited to present significant features of the 2½ hour examination telescoped into 15 minutes (Department of Zoology Library).

Autopsy

Gross morphology. Of the 120 birds used in the first experiment, 58, or almost half,were examined post mortem; the gizzard, intestine and caeca of each were weighed and the lengths of the intestine and caecum were measured.

In the second experiment the gizzard, intestine and caeca were opened and washed before weighing, as much as possible of the contents being removed. The diameter of intestine and caecum was also recorded, and thick sections of each were examined under the dissecting microscope. The lengths of several of the villi were measured using a micrometer eye-piece, and the average noted. The gonads were also weighed.

These findings, with the exception of the lengths of the villi,

were recorded throughout the third experiment also.

The intestino-caecal junction was examined in one case, longitudinal incisions being made and the epithelium and muscular wall inspected under the dissecting microscope.

Microscopic anatomy. A caecum from a bird kept at 23° C was fixed in 10% formol saline, postfixed in Zenker's solution and treated with iodine to remove the mercury. It was then deiodised with sodium thiosulphate and embedded in wax in seven transverse parts. Each part was sectioned at seven microns and some of the sections stained with Masson's trichrome stain. One caecum from a bird kept at 2-5° C for five weeks was also examined histologically, using the same stain.

RESULTS AND DISCUSSION

First Experiment

There was no difference in the original mean weight of birds in the two dietary groups. Birds on the low fibre diet gained weight progressively over the first 35 days, while those on the high fibre diet lost weight (Table 1). The latter lost weight even though they were eating a slightly greater weight and considerably greater volume of food, on the average, than those on the low fibre diet (Table 3). The increased volume resulted from the low density of Alpha Floc, the fibre that was added to the food. It seemed probable that the quail were eating as large a quantity as they were capable of.

Following this period a change in trend occurred. The mean food intake over the next 25 days diminished (Table 3) but the average weights of birds on both diets increased slightly (Table 1). It appeared that either the birds became more adapted to their particular diets or that they had reached adult size with a consequent reduction in nutritional demand, or both.

Between days 36 and 60 of this experiment, operations were performed on 80 of the birds; those on the low fibre diet were selected first, until it became apparent that those on the high fibre diet had ceased losing weight. The immediate effect of surgery was similar on all the birds, regardless of diet (Table 2). There were nine deaths

Table 1. Weight changes in quail held on diets of differing fibre content

	Original[3]	At day 35[4]			At Day 60[5]			At Day 74[6]		
	Mean Wt(g)	Mean Wt(g)	t	p	Mean Wt(g)	t	p	Mean Wt(g)	t	p
Control[1]	105	114	7.4	<.005	117	1.8	<.05	123	4.5	<.005
Experimental[2]	104	97	-4.9	<.005	101	2.1	<.05	111[7]	3.4	<.01

[1]Sixty birds held on diets of low fibre (laying mash alone).

[2]Sixty birds held on diets of high fibre (laying mash + 30% by weight of Alpha Floc, a cellulose fibre).

[3]At 6 weeks of age when received.

[4]After 35 days on given diets, birds held in groups of 5.

[5]After additional 25 days on given diets, birds held in groups.

[6]After additional 14 days, birds held individually.

[7]Mean and comparison based on sample of 30 birds.

Note: All weight recordings are mean weights over groups of 5 birds.

Table 2. Weight change in quail (in grams per bird) one week following surgery

	Sample size	Sham operation Mean	Range	Caecectomy Mean	Range
Control[1]	20	+3	0 - +6	-1	-3 - +1
Experimental[2]	20	-1	-2 - +4	-2.5	-3 - -2

[1]As in Table 1.

[2]As in Table 1.

attributable to the interference (see Appendix 2), but the remaining birds recovered quickly and showed only a slight loss in weight. This weight was regained subsequently, as can be seen by the overall weight gain demonstrated during this period of 25 days.

At day 60 the birds were transferred to individual cages and I hoped to compare the weights of the birds and their food intake before and after the change. This was straightforward in the case of the low fibre consumers, but owing to problems in obtaining Alpha Floc of a uniform consistency, not all of the birds on the high fibre diet could be included in the sample.

However, it does appear that the rate of increase in body weight accelerated (Table 1, final column), and that food intake increased in both groups (Table 3). In the case of the birds eating the high fibre diet, the increased intake was associated with the recovery from a period when the type of Alpha Floc was unsuitable; its density was so low that the birds were unable to eat sufficient quantities of food even, in a few cases, to survive. Most quail lost weight precipitously and fresh cellulose had to be obtained. The new material had a density that was greater than that of the original material, and apparently enabled the birds to ingest a greater weight of food per day. Eventually a stable state seemed to be reached (Table 3, column 5).

In general the quail ate a greater weight of food of high fibre content than of low, the weight of intake being sharply increased after substitution of the high density Alpha Floc. The average amount of food eaten during the five weeks in which half of the birds were kept in the cold environment may be seen in columns five and six (Table 3); here the

Table 3. Food intake in quail held on diets of differing fibre content

	Sample size	Mean wt of food eaten (g per bird per day)				
		Day 1-35	36-60	61-74	75-110[4]	
					Warm	Cold
Control[1]	60	16	11	15	13	22
Experimental[2]	60	17	15	21[3]	13	25

[1]As in Table 1.

[2]As in Table 1.

[3]Mean based on 30 birds.

[4]Based on sample of 15 birds in each category.

contrast between the low intake of 13 g per bird per day for both diets and the high intake (22 and 25 g) at low temperatures is obvious.

The cold environment had a considerable effect on the quail transferred into it, for these showed an initial weight loss of 5 to 10 g. After one week, however, this trend was reversed and the weight was regained or increased (Table 4). There was no gross difference between the weight changes of intact birds and those that were caecectomised, whether on a high or low fibre diet. The weight changes in the birds on a high fibre diet are distorted by the weight gains of birds recovering from the diet containing unsuitable Alpha Floc. Several of the birds on the high fibre diet died after transfer to the cold environment; these were apparently unable to consume the volume of food necessary to provide them with sufficient energy. These birds have not been included in Table 4. The deaths occurred whether the birds had been operated on or not (two controls, three sham-operated birds, and one caecectomised bird) and they were found to weigh between 70 and 80 g, compared with the 105 to 110 g for the remainder at the time.

Summarising these various aspects of the first experiment, it would appear that caecectomy in quail, as in chickens (Beattie and Shrimpton 1958), had no adverse effects on the birds. Further than that, even under conditions of stress due to low temperatures and a diet containing 30% cellulose, caecal loss was not responsible for mortality or morbidity.

However, it was felt that more needed to be known about the progressive changes in the birds under cold conditions, particularly the rate at which they occurred. It was therefore decided to take a group of

Table 4. Weight changes (in grams) in quail held at low temperatures

	Birds on low fibre diet						Birds on high fibre diet					
	No operation		Sham operation		Caecectomy		No operation		Sham operation		Caecectomy	
Sample size	9		9		10		7		4		6	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Original weight	114	7.3	124	6.1	123	10.2	102	9.0	113	2.3	106	8.4
Final weight	114	6.5	124	10.4	122	11.8	111	12.6	118	2.0	105	9.4
Wt change after 1 wk in cold	-5		-7		-9		-5		-8		-8	
Wt change in next 4 wk	+5		+7		+8		+14		+13		+7	
Net change	0		0		-1		+9		+5		-1	

intact quail and omit the dietary differences, since these did not appear to influence the caecal function at low temperatures. The birds were to be killed at weekly intervals to allow intestinal measurements to be made.

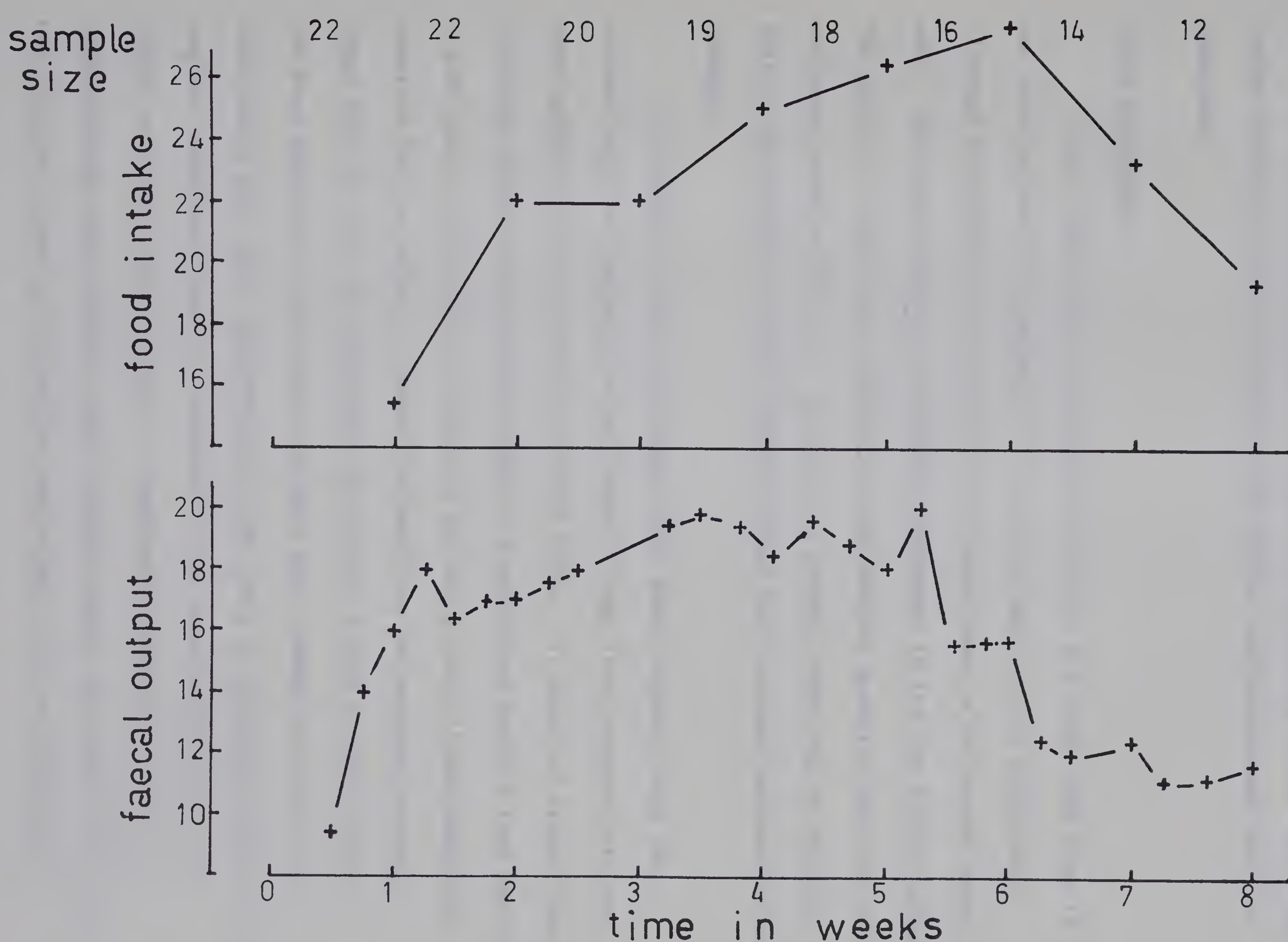
Second Experiment

With the birds all on a diet of turkey starter, it was found that the food intake, measured weekly, rose steeply from 14 g per bird per day at the time of admission to the cold environment, to a maximum of almost 28 g per bird per day after five weeks. Thereafter the intake declined until at the end of the experiment the birds were eating an average of 19 g per bird per day (Fig. 3). A similar trend was seen in the weight of faecal output, with the final daily average closely approaching the original condition. It was noted during weekly dissections that the birds had moulted irregularly during the first four weeks and that subsequently feathering was extremely dense.

The interesting outcome of this experiment was the rise and decline in amounts of food processed by the birds, occurring over what was a somewhat longer period of maintenance at low temperatures than that of the first experiment. It suggested that what was taking place might be a temporary phase in cold adaptation of the birds, which had not had time to be manifested in the five weeks of the first experiment.

However, it transpired that certain differences in conditions existed between the two experiments. The turkey starter had a higher protein content than the laying mash for which it had been substituted, and it was questioned whether this, or the difference in energy value associated with it, might produce some differences in the response of the birds. The calorific value of turkey starter was found to be 4.03 Kcal

Figure 3. Changes in food intake and faecal output in quail kept at low temperatures, expressed as grams ingested or expelled per bird per day


sample size
22
22
20
19
18
16
14
12
food intake
26
24
22
20
18
16
faecal output
20
18
16
14
12
10
0
1
2
3
4
5
6
7
8
time in weeks

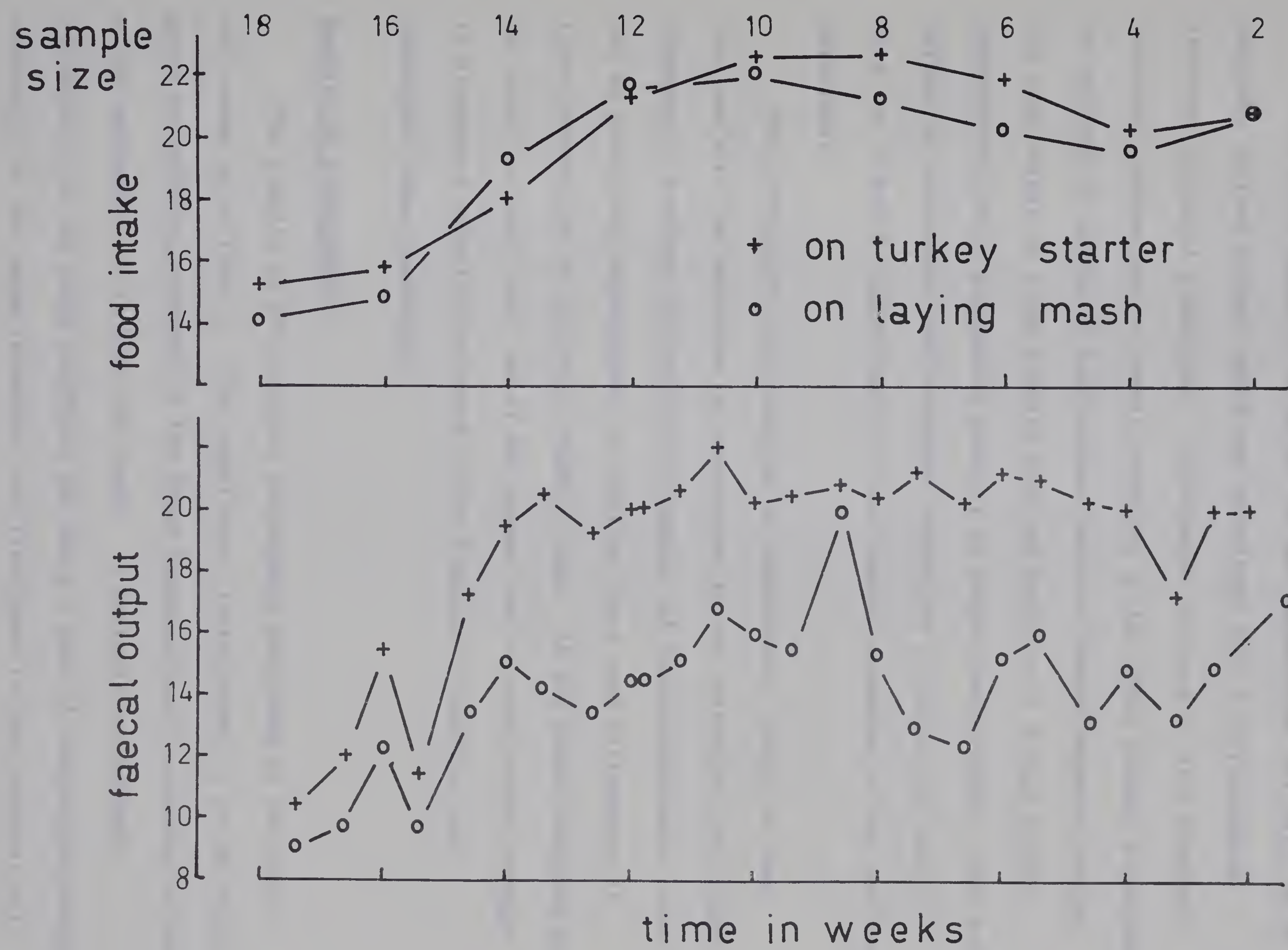
per gram (± 0.04) and that of laying mash was 3.91 Kcal per gram (±0.04). For this reason it was planned to repeat the foregoing experiment using turkey starter as food for half of the birds, and laying mash for the remainder.

Third Experiment

It was found that the intake of food for all birds rose from 14 g per bird per day to a maximum of 22 g, once again at the fifth week, although thereafter it decreased less steeply than in the second experiment. The faecal output was markedly different in the two dietary groups, the quail on laying mash producing a much smaller quantity than the ones on turkey starter (Fig. 4). As with the intake, there was no distinct fall in the weight of faeces produced after the five-week maximum had been reached.

In summary, these data suggest that quail without caeca can contend with low temperatures and diets of high fibre content with the same equanimity as that shown by intact birds. It might be argued that a cellulose product artificially added to a nutritious poultry food was not a good test of the effect of fibre in the diet, since it may have been possible for the birds to choose the mash from the mixture; however, a rough test of this, by separating the mixture (using a sieve) after it had been available to the birds for some days, showed that fibre still constituted only 30%. Nevertheless, some fibre is discarded before reaching the alimentary tract; it appeared in the water trays and on the faecal collecting paper beneath. A mechanical method of mixing and repelletising would provide a more reliable basis, but even in that case the fraction formed by the poultry mash might still be sufficient to

Figure 4. Changes in food intake and faecal output in quail kept at low temperatures on different diets, expressed as grams ingested or expelled per bird per day


sample size
18
16
14
12
10
8
6
4
2
food intake
22
20
18
16
14
+ on turkey starter
o on laying mash
faecal output
20
18
16
14
12
10
8
time in weeks

provide all the nutrient required.

The birds appeared to adjust to low temperatures initially by an increase in food intake, which was associated with a corresponding increase in faecal production. Differences in types of diet produced reactions independent of caecal presence; a high fibre content stimulated an increase in intake of food volume, and to a lesser degree of weight. The same weight of a low protein food was eaten as of a high protein preparation, but a diminished quantity of faeces was produced. This may perhaps be associated with increased extraction of energy per unit of food, or it may be associated with the chemical breakdown of the different materials.

The correlation with moulting is unexplained. Owing to some problems with the mechanism of photoperiod in the controlled environment chambers, a constant photoperiod throughout all three experiments could not be positively established; in addition there were differences in light intensities in different chambers used. At all events moulting did not occur in every case, and it did appear that the most marked changes in alimentary behaviour occurred in the presence of moulting and subsequent dense feathering.

Results of Radiography

The results of the contrast radiography performed on the quail are summed up in Table 5. The significant finding seems to be the retrograde peristalsis, observed in the large intestine only, pointing to this as the mechanism for filling the caeca. If peristalsis continues posteriorly in the small intestine and meets a wave of contraction moving anteriorly in the large intestine, the likelihood is that material will

Table 5. Stages in passage of barium meal administered to a quail

Time after administration	Position in gut
2 min	Barium filling gizzard, duodenum and small intestine (Pl. 1)
20 min	Barium in small intestine, large intestine and cloaca (Pl. 2)
25 min	Barium moving anteriorly in large intestine
40 min	Barium moving posteriorly to cloaca once more
2 hr	Most of barium evacuated through cloaca. Caeca seen to be retaining the material (Pl. 3)
2 hr 25 min	Gut empty

Plate 1. X-ray contrast photograph of a quail after ingestion of barium meal

Plate 1 Xray contrast photograph of a quail. Taken 10 min. after ingestion of a barium meal. Contrast material fills the small intestine. (Oblique view)

Plate 2. Barium meal after twenty minutes

Plate 2 Barium meal after 20 min. Duodenum is now empty, and contrast material has reached the cloaca. (Oblique view)

Plate 3. Barium meal after two hours

Plate 3 Two hours after ingestion of barium meal. Almost all the contrast material has been evacuated. (Oblique view)

be squeezed laterally into the caeca. However, the villi in the proximal portion of the caeca, being disposed in the manner they are (p. 34), would make entry of bulky fibrous particles difficult, but fluid material would be admitted readily.

Other interesting findings were the length of time for the "meal" to pass through the entire gut, and the fact that the caeca did spontaneously evacuate their contents. Caecal faeces are produced relatively infrequently in galliform birds, early morning being suggested as the usual time, although observations have been made on other occasions, for example under conditions of stress (Zwickel, F., pers. comm.).

Autopsy Results

All the birds were killed at the same time in the first experiment. Both the intestine and the caeca of quail kept at 2° C were bulkier than those of the birds kept at 23° C and measurements showed that the mean lengths were also greater. The caeca, regardless of diet, were nearly twice as long among birds from the cold environment as from those from the warm environment; likewise the intestinal lengths averaged 30% more than those from birds held in the warm environment. This increase (Table 3) was correlated with an increased food intake of both groups and the cold environment (Table 6).

Among caecectomised birds the site of excision was inspected. A slight development of the caecal stumps occurred in the birds held at 23° C but noticeable regrowth occurred in those at 2° C. The regrowth is presumably due to the difficulty of access to the junction of caecum with intestine, and failure to sever it close enough to the junction. The

Table 6. Post-operative alimentary dimensions in quail on different diets and held at different temperatures

	WARM						COLD					
	Low fibre			High fibre			Low fibre			High fibre		
	No op.	Sham op.	No caeca	No op.	Sham op.	No caeca	No op.	Sham op.	No caeca	No op.	Sham op.	No caeca
Number of birds	5	6	5	5	6	5	5	6	5	3	3	4
Mean lengths (mm)												
Caecum	51	51		52	57		104	95		97	93	
Intestine	360	375	350	390	365	360	496	460	488	510	500	457
Lengths (mm) in dietary groups	Mean	Range		Mean	Range		Mean	Range		Mean	Range	
Caecum	51	45- 60		55	45- 70		100	80-110		95	80-110	
Intestine	360	320-440		372	350-400		481	380-530		489	430-580	
Lengths (mm) in temperature groups		Mean			Range			Mean			Range	
Caecum		53			45- 70			98[1]			80-110	
Intestine		366			320-440			482[1]			380-580	

[1]Weighted average.

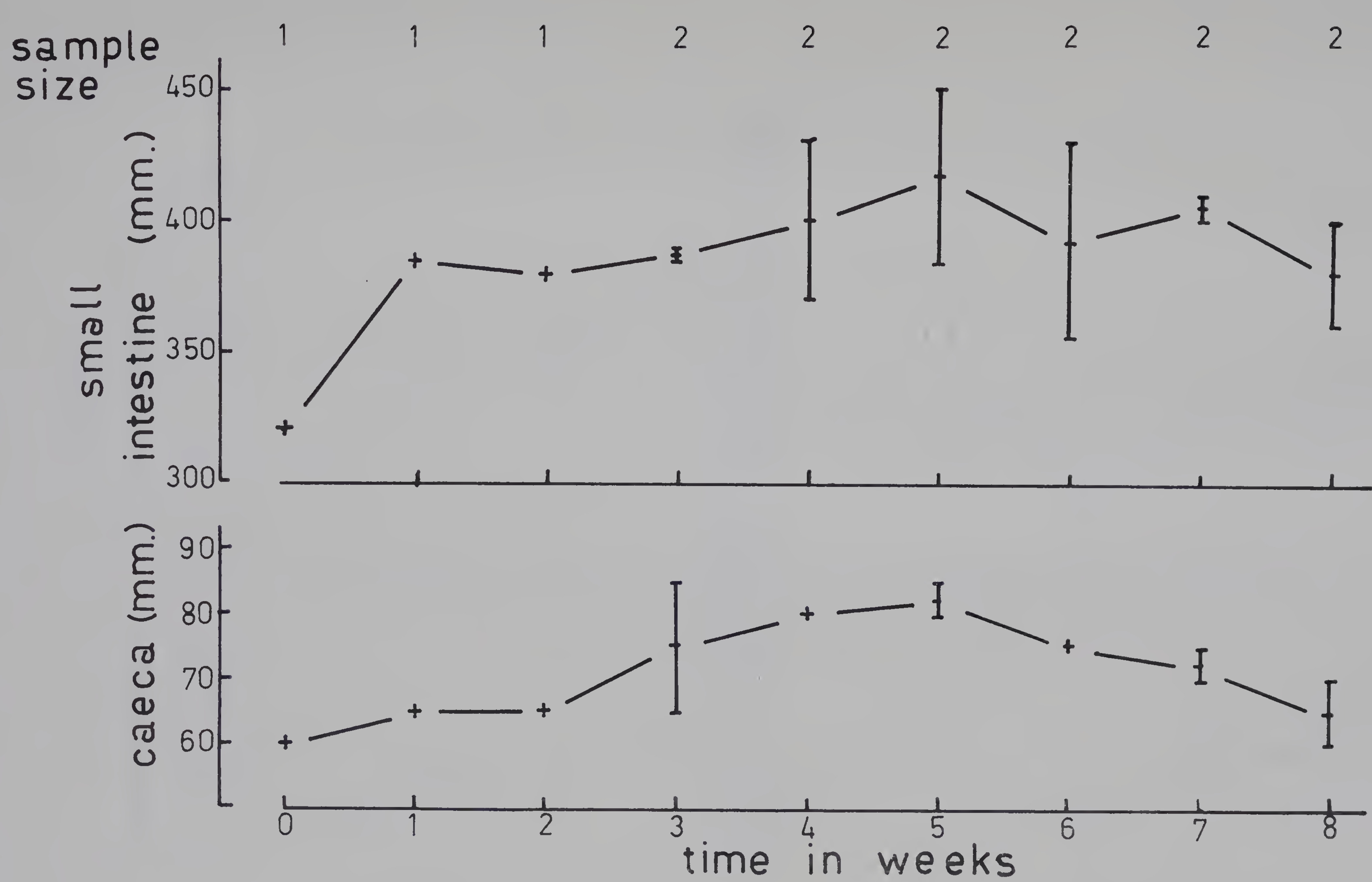
greater development of caecal stumps in the cold-adapted birds emphasises the stimulus of cold (possibly via increased food intake) to gut enlargement (Fig. 9).

Intestinal and caecal lengths in the second experiment did not attain the lengths recorded in the first experiment (Fig. 5). Small intestine and caeca increased by 33%. Changes in lengths of these organs were correlated with changes in food intake. The length of the small intestine increased to a maximum at the same time as the caecal length, but the curve produced is irregular, which may perhaps be accounted for by the small sample size. The villi in the proximal part of the caecum underwent an elongation, the maximum size reached being approximately 0.65 mm, decreasing to 0.5 mm once more at the end of the experiment.

It is possible that the difference between the dimensions recorded in this experiment and the first one were due to one of two factors. In the first place the feed given was a high protein mixture, of a greater calorific value than that used previously (p. 21). In the second place some difficulty was experienced in maintaining required temperatures in the controlled environment chamber. Several days elapsed before a temperature of 2° C was reached, and even then it regularly rose to 5° C during the middle part of the day.

In the third experiment, as can be seen from Figure 7, the intestine increased in length from approximately 350 mm to 400 mm and subsequently decreased. The caeca showed a sporadic enlargement throughout the birds, from an average of 50 mm at the beginning of the experiment to approximately 70 mm at the end. An increase in length towards the end of the experiment, following the expected decrease after the fifth week,

Figure 5. Changes in lengths of small intestine and caeca in quail kept at low temperatures



sample size
1
1
1
2
2
2
2
2
2
small intestine (mm.)
450
400
350
300
caeca (mm.)
90
80
70
60
0
1
2
3
4
5
6
7
8
time in weeks

Figure 6A. Changes in lengths of small intestine and caeca in quail kept at low temperatures on a 26% protein diet (turkey starter). Two birds killed each week.

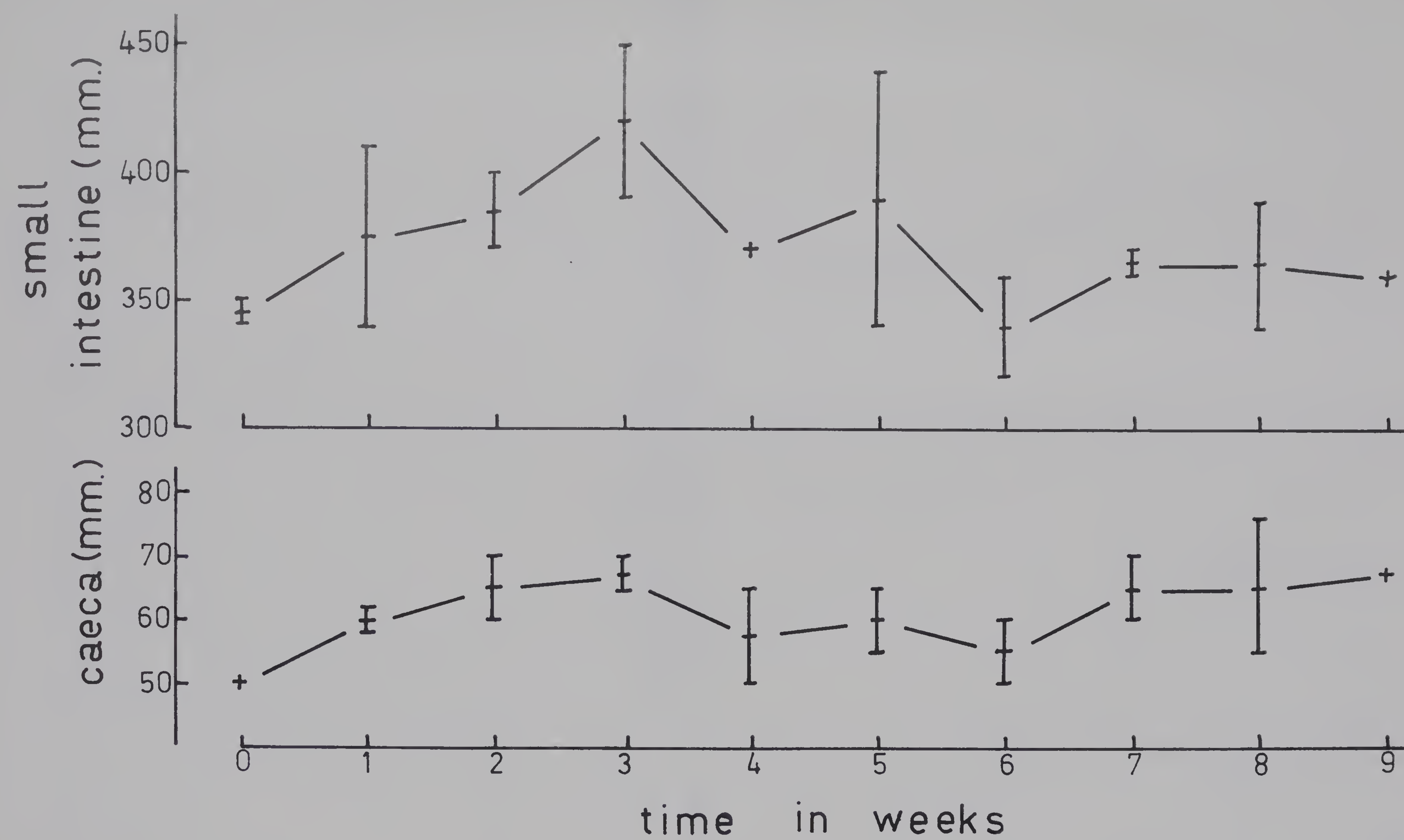
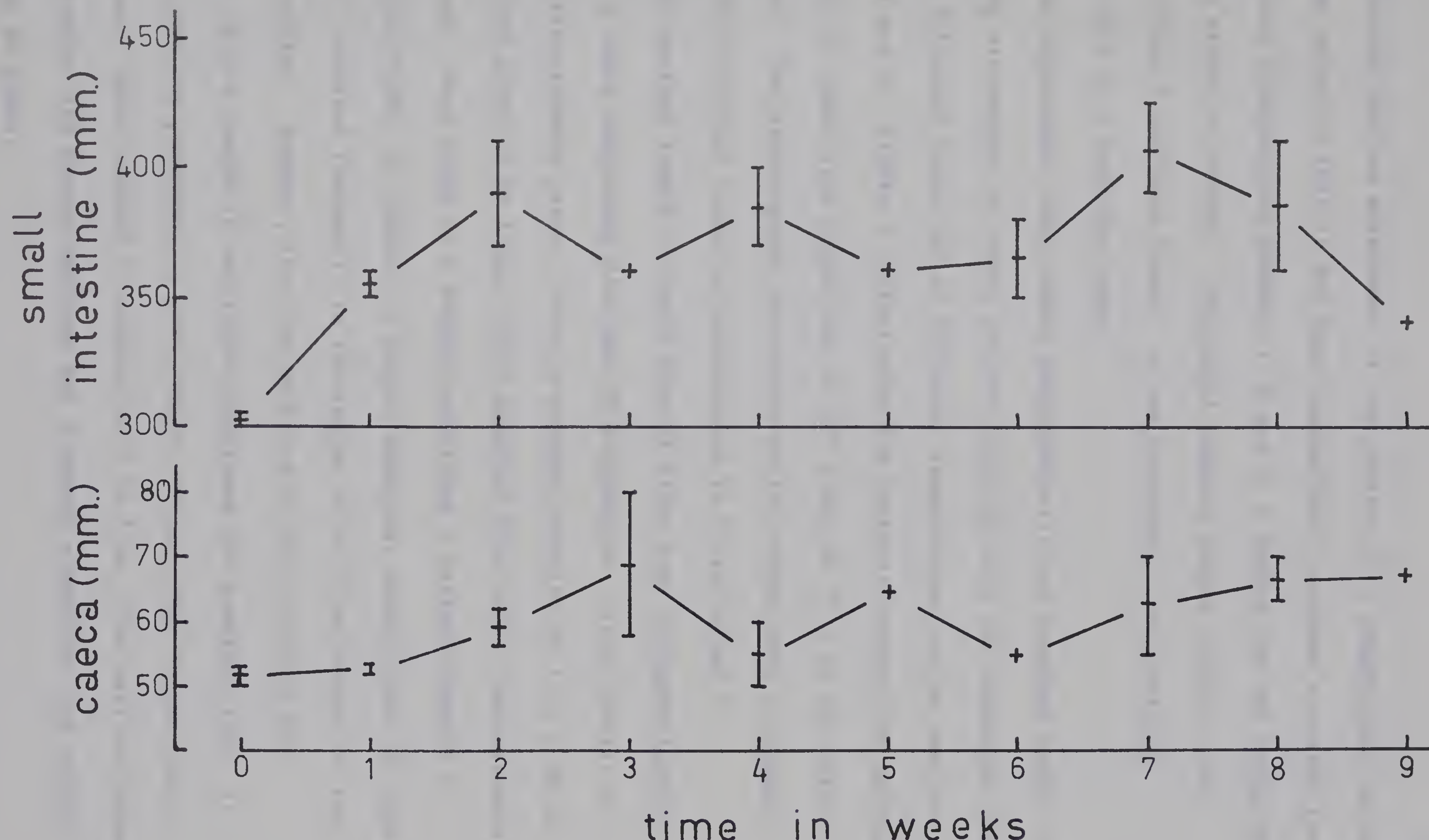

small intestine (mm.)
450
400
350
300
caeca (mm.)
80
70
60
50
0
1
2
3
4
5
6
7
8
9
time in weeks

Figure 6B. Changes in lengths of small intestine and caeca in quail kept at low temperatures on a 16% protein diet (laying mash). Two birds killed each week.


small intestine (mm.)
450
400
350
300
caeca (mm.)
80
70
60
50
0
1
2
3
4
5
6
7
8
9
time in weeks

was correlated with an attainment of the desired 2° C temperature in the cold room; prior to this it had been impossible to achieve a steady low temperature, fluctuations between 3° C and 7° C during the day being the customary state of affairs. The caecal weights varied slightly, but failed to show a definite trend. It was noticeable that moulting occurred only in a very few cases.

The appearance, when opened longitudinally and examined under the dissecting microscope, of caeca and the junction with the intestine from birds on different diets and at different temperatures can be seen in Figures 7 and 8. Figure 9 illustrates the contrast between the external appearance of caeca from birds kept at 23° C and at 2° C in the first experiment. The histological appearance of the caecum when sectioned through the different zones is demonstrated in Plates 4 and 5.

The average length of caeca from 22 birds kept at approximately 23° C on a mixed laboratory diet was 50 millimetres. They consist of three distinguishable parts: first a proximal section of 1 or 2 mm in diameter and about 10 mm long, richly supplied with villi, approximately 0.5 mm long. Next there is a region containing a variable number of longitudinal folds, or ridges, of mucous membrane, usually four or five in number, situated frequently in the region 10 or 20 mm distal to the villous section. However, they can be found in every part of the remainder of the caecum if sufficient specimens are examined (Fig. 7). The villi are not prominent in this region, nor are they in the third, dilated part, which reaches a diameter of 5 to 7 mm. The wall is thinner in this region, the mucous membrane has a smooth appearance and usually is lacking in folds.

Figure 7. Internal appearance of caeca (actual size) from individual quail, showing variability in mucosal structure and the changes observed at low temperatures

A - Kept at 23° C on experimental diet
1 - villous zone; 2 - ridged zone; 3 - dilated zone

B - Kept at 23° C on control diet

C - Kept at 23° C on control diet

D - Kept at 23° C on experimental diet

E - Kept at 2° C on control diet

F - Kept at 2° C on control diet

G - Kept at 2° C on experimental diet

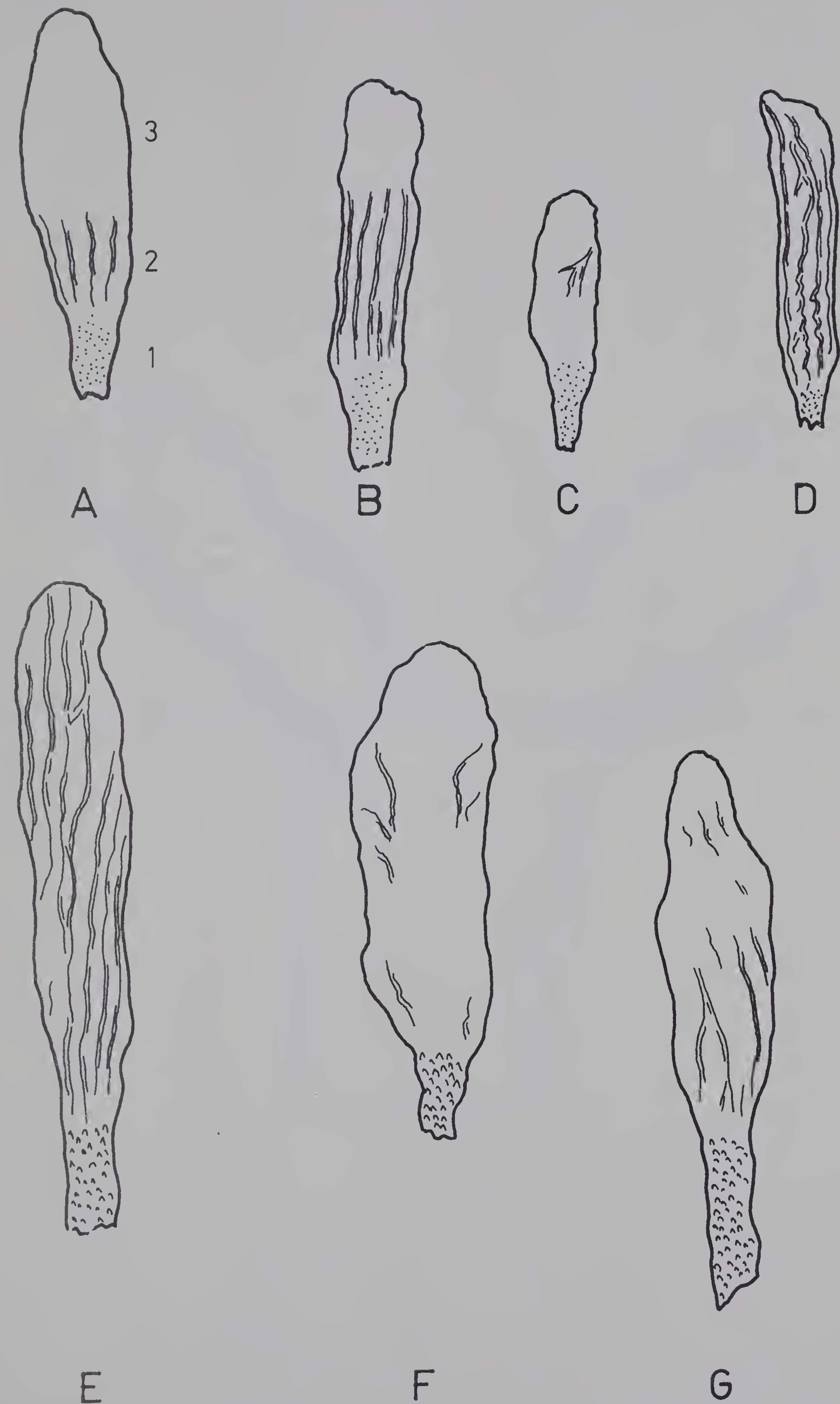

3
2
1
A
B
C
D
E
F
G

Figure 8. Internal appearance of junction of caeca and intestine in the quail (approximately 15X)

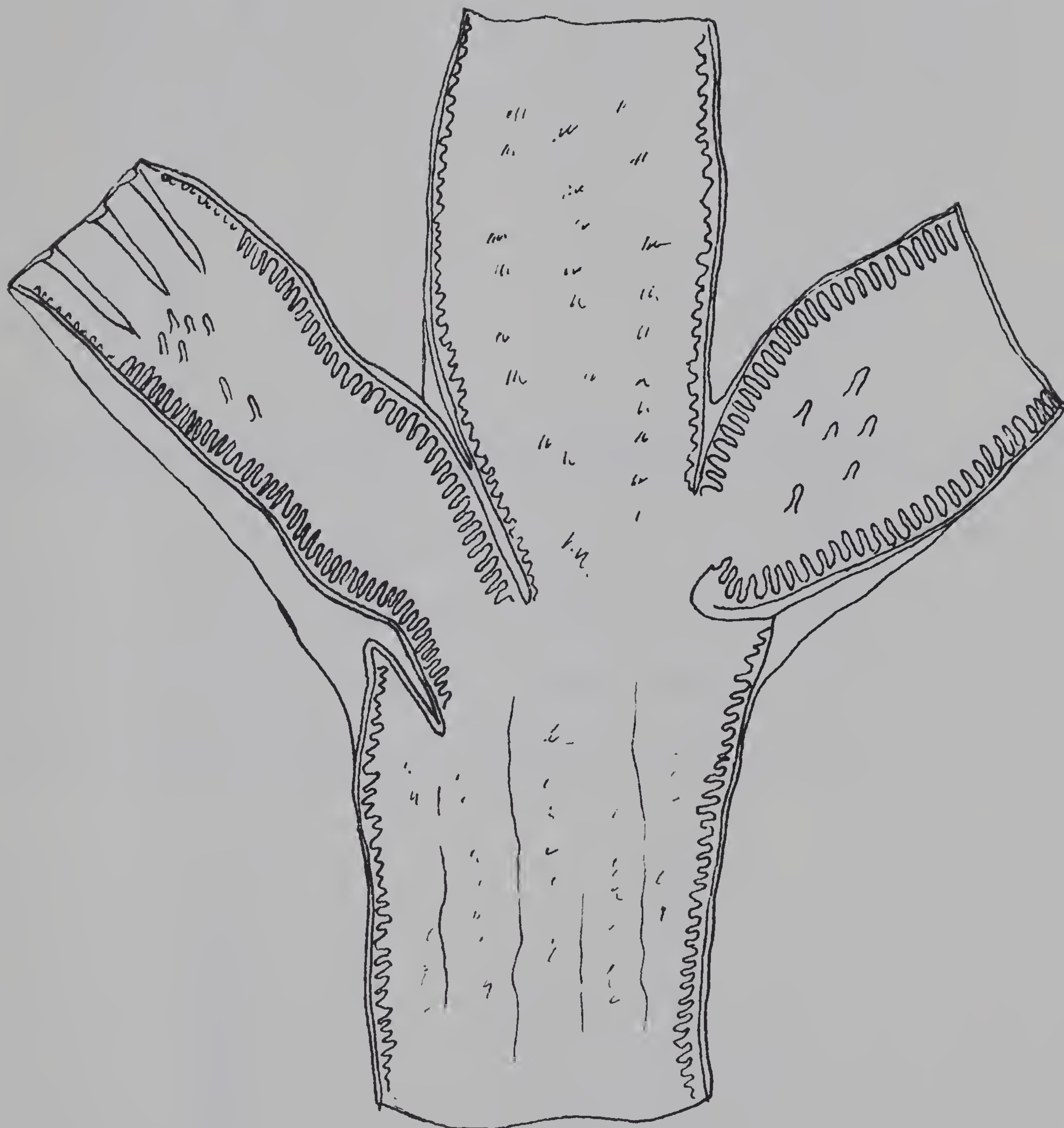


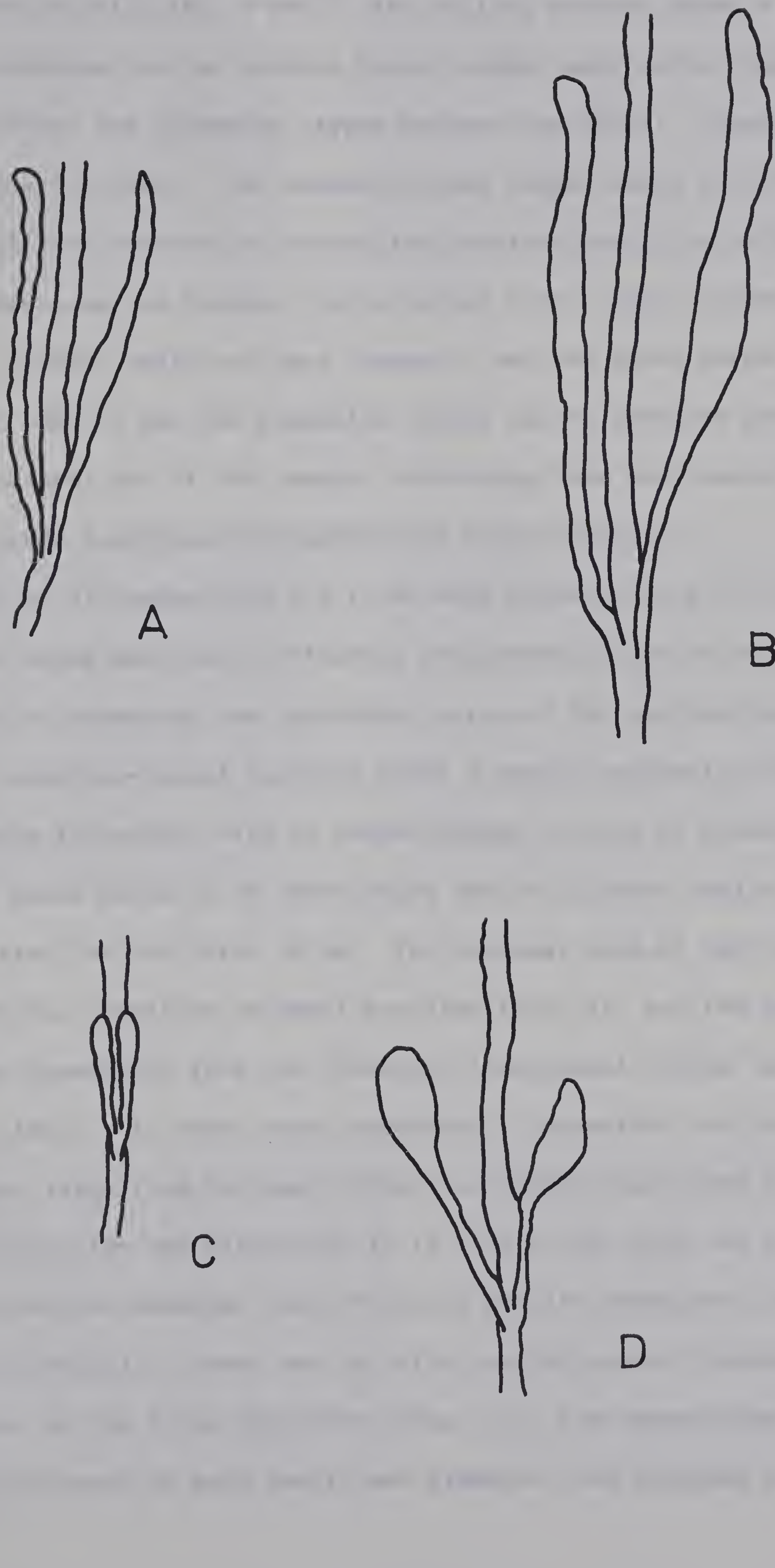
Figure 9. Appearance of representative caeca after dissection from intestine (first experiment). Actual size

A - From quail on control diet kept at 23° C

B - From quail on control diet kept at 2° C

C - Caecal stumps showing moderate regrowth at 23° C

D - Extreme case of regrowth of caecal stumps at 2° C


A
B
C
D

Microscopically (Pl. 4 and 5) the villous section shows a deep columnar epithelium with an obvious brush border, many goblet (mucus producing) cells, and glandular crypts between the villi. Lymphocytic aggregations are present. The second, ridged region shows shorter villi, and in the dilated section the epithelium consists merely of extremely shallow prominences and troughs, all provided with a short columnar epithelium. Goblet cells are less frequent, and the brush border less obvious, but both it and the glandular crypts can be detected from proximal to distal end of the caecum, indicating that both secretion and absorption could take place throughout the entire surface.

Plainly, if comparisons are to be made between caeca of birds killed after being kept under differing environmental conditions, one must be sure of examining the equivalent parts of the various specimens.

The intestino-caecal junction shows a smooth continuity from small to large intestine, with no sudden change in size or shape of villi. The caeca arise at an acute angle and are closely applied to the small intestine for the first 10 mm. The proximal ends of the caeca project into the intestine as small papillae (Fig. 8), and the necks of the papillae presumably form the "muscular ileo-caecal valves" mentioned by Sturkie (1965). It would seem anatomically impossible for these to close off the large from the small intestine (Newton and Gadow 1896) but by their contraction and dilatation it is likely that they can govern entry of intestinal material into the caeca and its subsequent discharge.

Macroscopically, there was no effect on the caeca of dietary fibre content in the first experiment (Fig. 7). Low temperatures produced an increase in both length and diameter, and internal examination

Plate 4. Photomicrographs to show caecal structure under different conditions of temperature

A - Villous zone. 23° C (40X)

B - Villous zone. 2° C (40X)

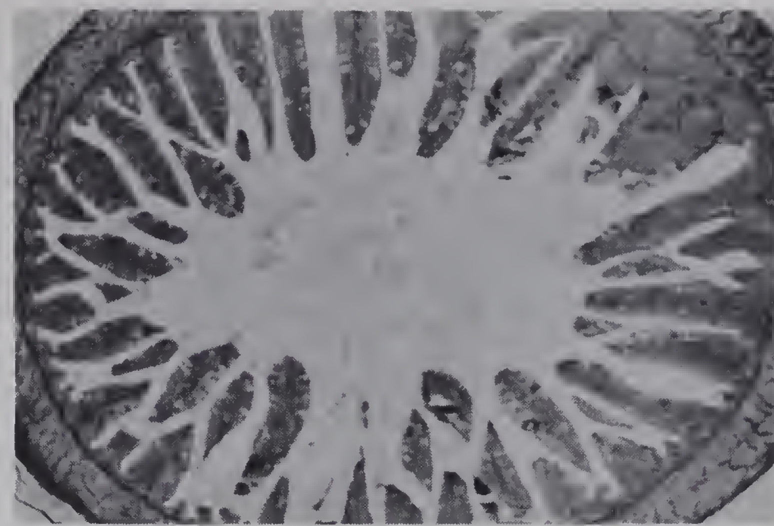
C - Villous zone. 23° C (100X)

D - Villous zone. 2° C (100X)

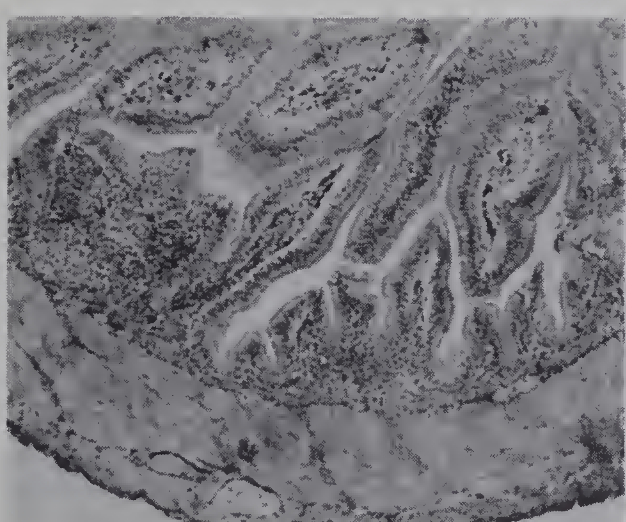
E - Ridged zone. 23° C (100X)

F - Ridged zone. 2° C (100X)

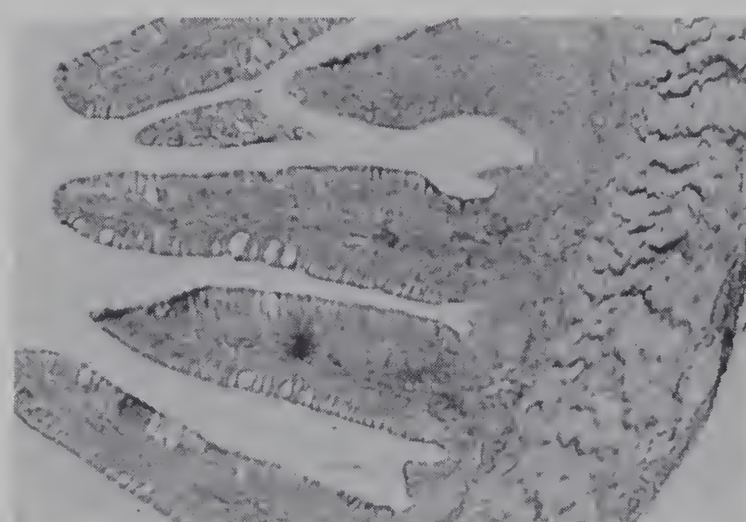
A



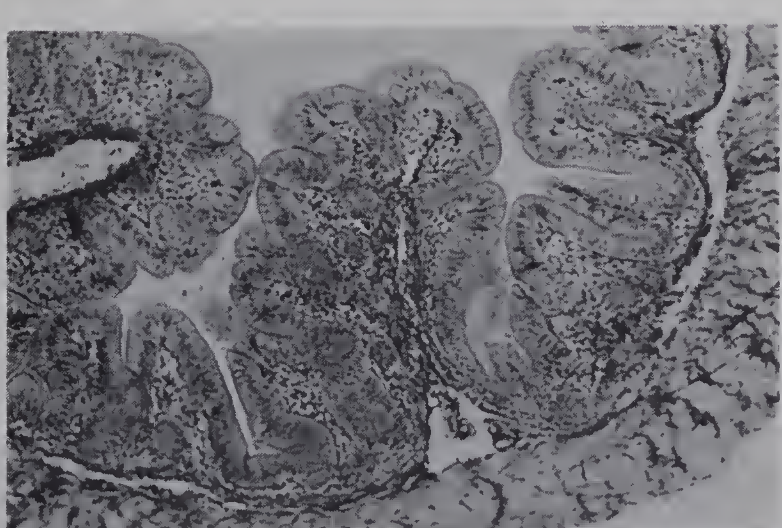
B



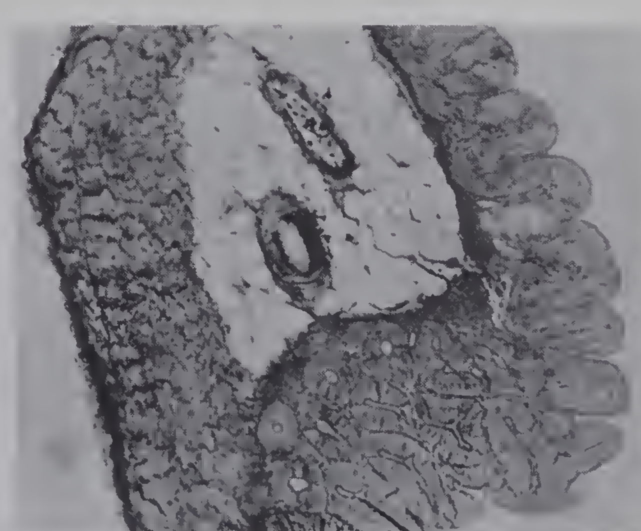
C



D



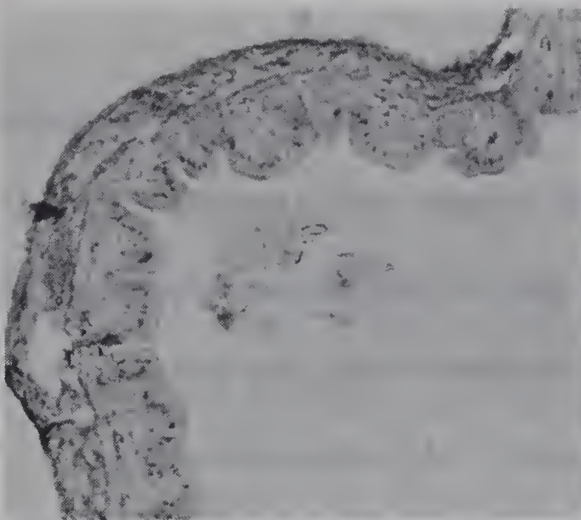
E



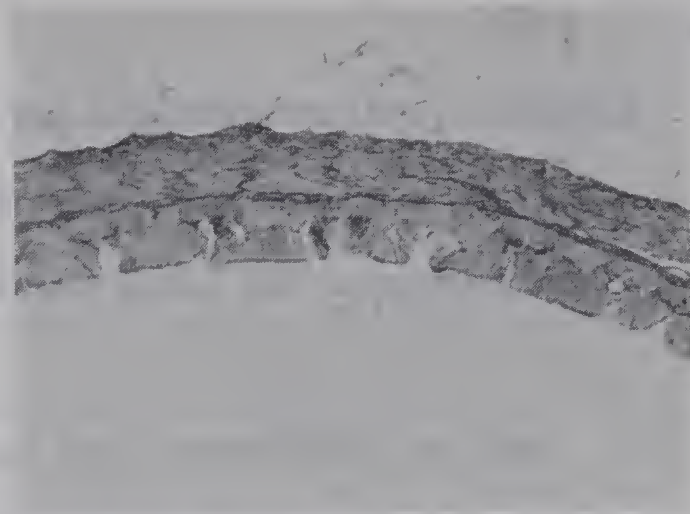
F

Plate 5. Photomicrographs to show caecal structure under different conditions of temperature

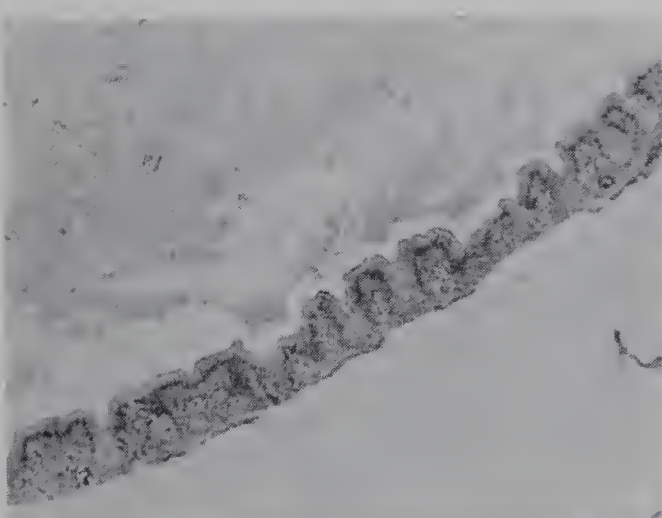
A - Dilated zone	23° C (100X)
B - Dilated zone	2° C (100X)
C - Terminal zone	23° C (100X)
D - Terminal zone	2° C (100X)
E - Crypts of villous zone	23° C (250X)
F - Mucous membrane of dilated zone	23° C (250X)



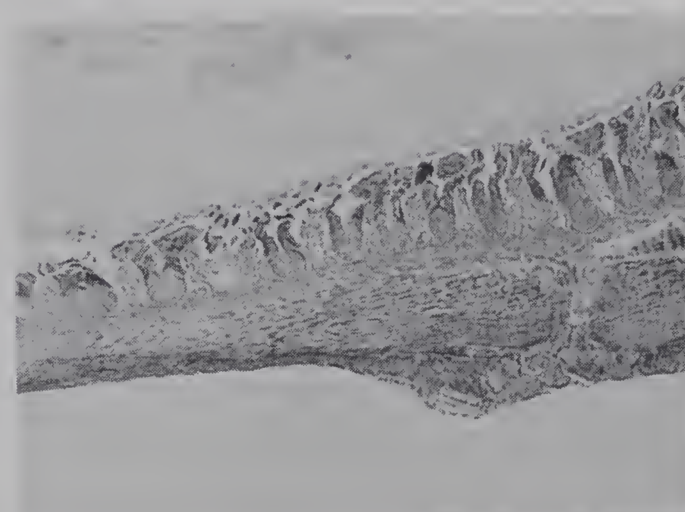
A



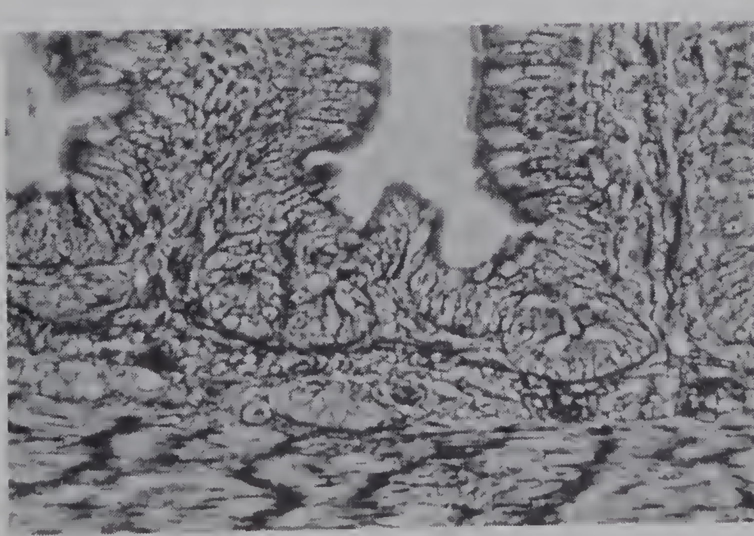
B



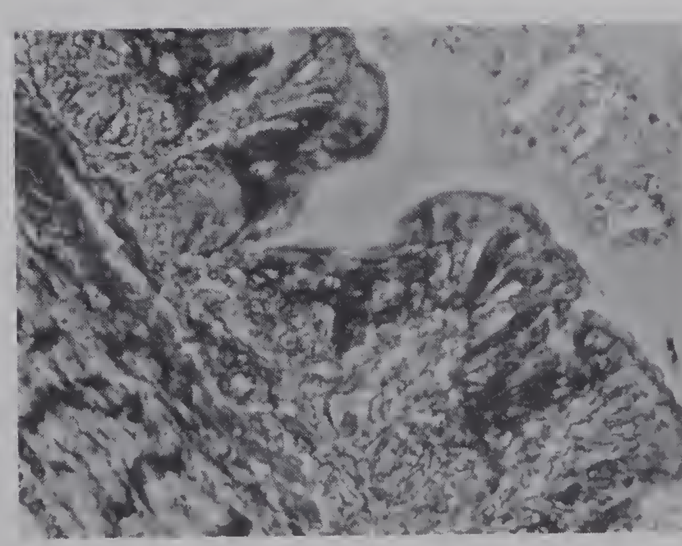
C



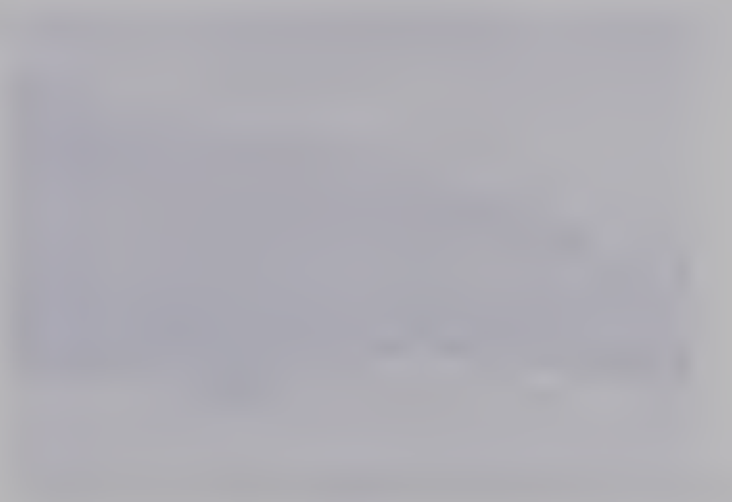
D



E



F



revealed a hypertrophy of the villi in the proximal section, although the diameter of the region was not increased. The greatest overall enlargement occurred in the smooth, dilated zone, but longitudinal ridges were not obliterated.

Microscopically, the same regions are identifiable in the specimens from the cold environment as from the warm one (Pl. 4 and 5). Each region is larger than the comparable one from the warm environment, and the ridges are lower, suggesting that dilatation has occurred.

CONCLUDING DISCUSSION

The aim of these series of experiments was to look directly at the function of the caecum in some member of the Galliformes, to discover if the caecum was necessary to the bird's existence, and, if not, what disadvantages would accrue from caecectomy. Some of the birds were subjected to low temperatures and a high fibre diet because of the correlation that exists between the possession of unusually large caeca and the ability to survive low ambient temperatures while subsisting on a high fibre diet.

No conclusive discovery is claimed for the outcome of the series; the results on the whole were negative: caecectomy in quail appeared to bring with it no disadvantages. On the other hand, caecal enlargement at low temperatures suggests that the organ, while not essential to health, is far from vestigial.

Inspection of the structure of the caecum in different individuals led to the appreciation of relationships between it and the remainder of the alimentary tract; it showed the narrow neck, lying almost parallel to the small intestine and filled with the projecting villi of the lining epithelium. It indicated the extreme difficulty that intestinal contents would have to enter the caecum during normal passage along the gut from gizzard to cloaca. It showed the main body of the caecum, thrown into ridges and lined with absorptive and secretory epithelium. Following the course of intestinal contents by X-ray photography threw a fresh light on concepts of caecal activity and led to the belief that the caecum is

in fact filled by antiperistalsis in the large intestine, which appears to direct the contents backwards into the caeca, squeezing it through the villous meshwork of the openings.

The results of the quail studies are consistent with previous knowledge of grouse caeca in that changes in bulk of food ingested are associated with changes in caecal length in both families.

Taking into consideration the results of digestibility experiments which were performed on spruce grouse by Pendergast, and willow ptarmigan by Pulliainen, it does not appear that cellulose is greatly used by the birds.

The extraordinary development of the caeca in birds feeding on green vegetable matter cannot, however, be ignored. It seems most probable that this occurs in response to the great bulk of green feed necessary to provide sufficient energy, especially in winter, and that the caeca function as adjuncts to the small intestine, in the continuing digestion of basic food materials.

It might be asked what the purpose could be of development of blind sacs in contrast to further enlargement of the small intestine, and I postulate that the answer lies in the mechanism of separation of food material by the structures comprising the caecal ducts, or openings. Radiography suggests that the caeca fill by retrograde peristalsis in the large intestine, onward peristalsis in the small intestine occurring at the same time. While the neuromuscular coordination required for this complex activity seems difficult to visualise, the mechanical effectiveness is quite clear. No other method in the absence of valves seems feasible, and inspection of the gut reveals no morphological valves. The

circular muscle at the proximal end of the caecum may well act as a functional valve in retaining material in the caecum, allowing ingress and egress by relaxation, but could not affect the movement of material in the intestine.

The enlarged villi in the proximal zone are very interesting, since at first glance they do not seem well placed for absorption, commonly accepted as their normal activity. However, they may have a greater mechanical importance in this situation, since their interdigitating fingers seem to form a sieve which could allow liquid intestinal contents through, and prohibit the entry of coarse fibrous material with which the large intestine is packed.

I submit that by eliminating this particulate matter the digestion of the remaining fraction conceivably is greatly increased in efficiency. Separation of this type was described in spruce grouse by Pendergast (1969) as occurring in an intermittent fashion when the ventriculus appeared to release first the liquid fraction of macerated food then a bolus of fibrous material in the duodenum, and would have a similar but less complete role in the intestine as it apparently has in the caecum.

Submicroscopic particles of cellulose and lignin obviously do enter the caeca, as demonstrated by chemical analyses (Pendergast and Boag 1971), and it appears that some of this material is fermented and digested (McBee and West 1969). However, in proportion to the quantity of fibre that is expelled I suggest that this is a relatively minor aspect of the caecal function.

When the natural history of the birds is considered, it becomes clear that this suggested modification of the usual digestive direction

would be an efficient way of processing the large quantities of food necessary to the birds when feeding on green vegetation. Sudden flight occasioned by danger, for example, would be hampered by excess weight, and it is important that food be processed quickly in order to rid the bird of weighty indigestible materials. This almost certainly rules out bacterial fermentation on a large scale. However, a mechanism for separation of nutrient residues from the waste fibrous material would be an additional advantage. The presence of caeca seems to offer a useful solution; studies of digestion in pheasants using Chromium 51 as a marker (Duke 1967) have shown by differential concentration of the radioactive material in caecal and intestinal faeces that foods diverted to the caecum were absorbed to a greater degree than in the intestine. Virtually without interrupting the flow of intestinal material, the semi-digested portion can be sidetracked for final processing and absorption, and the fibrous material expelled. It seems likely that this function has been secondarily developed in herbivorous birds, and could feasibly account for the disparity in caecal development between them and the avian majority.

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APPENDIX 1

GENERAL ANAESTHESIA FOR QUAIL

There are several reports of anaesthetics used in birds, including ether, Halothane, trichlorethylene and methoxyflurane ("Fluothane") by inhalation, and pentobarbitone ("Nembutal") by intraperitoneal and intravenous injection.

Hagen (1964) describes a simple apparatus for successfully administering "Fluothane" to small mammals. I tried this technique with the quail, but found that not only did I need more than half my attention on the apparatus in frequently adjusting the flow of air bubbling through the anaesthetic, but 50% of the birds died in spite of this. There seems to be a very narrow margin of safety between sleep and death.

Beattie and Shrimpton (1958) describe the use of "Nembutal" in young chickens, given intraperitoneally at the rate of 30 mg per kg of body weight, without remarking on any problems, but I found that some birds were not adequately anaesthetised by this dose, whereas others died; apparently there are noticeable individual differences between birds in their reactions to drugs. A disadvantage of parenteral anaesthesia is that the dose cannot be adjusted in the same way that it can during inhalation.

Ether dripped on to cotton wool covering the nostrils also gave unpredictable results and, in addition, required an assistant to administer the anaesthetic. Jones (1966) describes the successful use of Halothane in turkeys, but he employed a standard anaesthetic machine,

including positive pressure apparatus for inflating the lungs with oxygen when apnoea occurred. This indicates that some of his birds also suffered from an excessive dose of the anaesthetic.

Hollingsworth and Howes (1965) compared parenteral and inhalational anaesthetics and they came to the conclusion that none was entirely satisfactory, and that the best technique to use for gastro-intestinal surgery was local anaesthesia. I agree with their findings.

I did find that the presence of an assistant was advisable during the caecectomies, because any sudden restless movement of the bird at the time when the caecum is being removed and the stump sutured can mean that the clamp slips off or the ligature pulls out, causing the stump to disappear from sight. The laparotomies, however, can be performed quite readily without any restraint other than those described.

APPENDIX 2

SURGICAL MORTALITY

There were nine deaths directly attributed to operations on the quail, all occurring in relation to the caecectomies, and not the sham operations.

Causes of death were found to be:

1. Asphyxia (during operation)

2. Shock (collapse and death just after completion of the operation)

3. Faecal peritonitis due to leakage of the caecal stump (two cases)

4. Intestinal obstruction due to adhesions

5. Intra-intestinal haemorrhage

6. Intestinal obstruction due to atresia, the suture of the caecal stump being so close to the junction with the intestine that resultant fibrosis narrowed the intestinal lumen excessively.

7. Intestinal obstruction due to volvulus

8. Septic peritonitis

These nine deaths out of eighty operations represented a very low mortality rate in comparison with that obtained during previous investigations of general anaesthetics (see Appendix 1) and it was felt that local anaesthesia was far preferable in a situation where oxygen, intubation facilities and resuscitation equipment were not available.